Distribution and Persistence of American Chestnut Sprouts, *Castanea dentata* [Marsh.] Borkh., in Northeastern Ohio Woodlands[1]

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ABSTRACT. **Sprouts and stumps of American chestnut, *Castanea dentata* [Marsh.] Borkh., were mapped from data collected at three forested sites of varying size and historical background in Cuyahoga County of northeast Ohio to compare the species' present distribution with that of its historical distribution in the mentioned areas. Sprouts were absent from one site despite a dense population of remnant chestnut stumps. Distribution of sprouts within the two remaining sites was sparse except for localized high concentrations. In addition to the aggregated pattern, sprout distribution was somewhat shifted from chestnut stump distribution indicating that such stumps are not the direct sources of regenerative tissue, but were the likely seed sources for younger, active root systems presently generating sprouts. Data collected to assess sprout location in relation to canopy changes indicated a continued association of American chestnut with white oak, *Quercus alba*, and red oak, *Quercus rubra*. Variations in sprout distribution are related to past land use and the subsequent stage of development of each site. The absence of sprouts from the old growth forest is attributed to competitive exclusion by shade tolerant species—mainly sugar maple, *Acer saccharum*, and American beech, *Fagus grandifolia*. Although comparisons of sprouting rates versus death rates over a three year period indicated a 30% increase in the number of chestnut stems giving the appearance of a growing population, succession toward beech-maple forests was evident at all three sites as is the case in many forested areas of this region.**

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INTRODUCTION

At the beginning of this century, eastern deciduous forests displayed stands of American chestnut, *Castanea dentata* [Marsh.] Borkh., that ranged over 200 million acres from Maine to Georgia west to the Mississippi (Peattie 1950). The chestnut's tolerance of a wide range of soil conditions and temperature differences made it not only a climax species of the oak-chestnut forest in its primary range of the southern Appalachians and Northern Blue Ridge area, but it was a major constituent of the adjacent mixed mesophytic forest. Chestnut could also be found as a climax species in physiographic climax communities as well as in developmental communities within the western mesophytic forest and the beech-maple forest of the glaciated area just north (Braun 1950). Like a number of the deciduous species tolerant of colder temperatures (beech–*Fagus grandifolia*, red maple–*Acer rubrum*, sugar maple–*Acer saccharum*, white oak–*Quercus alba*) the expanse of chestnut had continually broadened northward for approximately 25,000 years with the retreat of the Wisconsin Glacier (Sears 1930). Within the area of Cuyahoga County, OH, recognized as a part of the beech-maple climax region, are remnants of oak-chestnut communities. Capable of growing on the young podzolic soils of glaciated territory, such communities may have been able to sustain themselves for as long as the topographic form upon which they thrived endured. Now these communities show evidence of transition toward the beech-maple climax species of the area (Braun 1950). Important to note is that this region's forested areas are of secondary growth following the decline of agriculture and the onset of urbanization and industrialization. The character of the soil that would likely have maintained more of these oak-chestnut communities as self-sustaining physiographic forests has been altered toward more mesic conditions through grazing, plowing, and fire suppression.

To compound the dynamics of forest succession in these oak-chestnut communities, the invasive fungus subsequently identified as *Cryphonectria parasitica* [Murr.] Barr (formerly *Endothia parasitica* [Murr.] And.) was inadvertently introduced to America via a shipment of lumber from the Orient (Peattie 1950). Since its introduction, perhaps as early as 1905 (Merkel 1905), the blight fungus quickly spread throughout the chestnut range, killing 3.5 billion chestnut trees (Nash 1988) faster than they could reproduce and leaving little chance for blight resistance to evolve. The character of the forests in which chestnut dominated have changed significantly as young oaks filled the voids or beech and maple took root in forests already showing transition toward more shade-tolerant species (Braun 1950). In later attempts to halt the spread of blight and retrieve valuable lumber, the Civilian Conservation Corps (CCC) and the Work Projects Administration (WPA) had many chestnuts felled, thereby further reducing potential genetic sources of blight resistance. Because few chestnuts reached sexual maturity in the presence of the blight, vegetative regeneration of tissue from living root crowns has been the only means of eluding extirpation from Ohio.

There are a number of conservation efforts of the American chestnut. In addition to its obvious use as a food resource for wildlife and for its rot-resistant lumber, there are important insights to be gained. Scientifically, the fungal epidemic and the response of *Castanea* offer a continuing glimpse into a prolonged, adversarial,

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host-pathogen relationship. The diminution of a dominant species in such a short period of time makes clear the impact of human endeavors and the need to preserve this species and others through an interdisciplinary approach in an effort to secure biodiversity. Perhaps most apparent is the need for controls in the movement of organisms.

Two promising directions of research are presently being pursued with the goal of returning the American chestnut to a useful canopy tree. One approach is through hybridization. The American Chestnut Foundation has been crossing Chinese chestnut (*Castanea mollissima* Bl.) and Japanese chestnut (*Castanea crenata* Sieb. & Zucc.) with American chestnut in an attempt to combine blight resistance, a characteristic of the Oriental species of *Castanea*, with the favorable lumber qualities of the American chestnut in the resulting hybrid. The second approach attempts to exploit a natural occurrence of less virulent strains of *C. parasitica*. Hypovirulent strains carry a virus-like double stranded RNA molecule referred to as HAV or hypovirulence associated virus (Shapiro et al. 1991) which invades the cytoplasm of other strains of the blight after anastomosis (Anagnostakis 1987). The presence of dsRNA in hypovirulent strains is associated with phenotypic distinctions from the original virulent types, such as reduced sporulation, reduced pigmentation, and superficial canker fermentation (Hebard 1982, Shapiro et al. 1991). Use of hypovirulent strains of *C. parasitica* have been tried as a biological control of chestnut blight in Connecticut orchards with some success (Anagnostakis 1990). Such efforts may eventually lead to the introduction of genetically altered chestnuts or weakened strains of the blight fungus into natural areas where American chestnuts previously existed.

MATERIALS AND METHODS

American chestnut sprout populations were observed in three forest sites in Cuyahoga County, OH. The sites are located within three reservations of the Cleveland Metroparks. These sites are the A. B. Williams Memorial Woods of North Chagrin Reservation, a ridge along a portion of Tinker's Creek in the Bedford Reservation, and an area just east of the Brecksville Nature Center in the Brecksville Reservation. Since the park's inception in 1917, the purchase of each reservation has afforded them protection from most disturbances. All study sites have a number of chestnut stumps. Sites at Bedford and Brecksville are secondary growth forests, while the A. B. Williams Memorial Woods display remnants of original forest altered only by climatic succession, not by farming or grazing (Williams 1949).

A grid was established at each of the three sites. In North Chagrin, the grid encompassed 7,200 m^2; in Bedford, 18,800 m^2; and in Brecksville, 32,400 m^2 (Figs. 1-3). The size of the grid was determined by natural or man-made boundaries. Each grid, by compass and meter gauge, was then divided into 20 m by 20 m quadrats. Each quadrat was traversed at 5 m intervals during late spring and throughout the summer in search of American chestnut stumps and sprouts.

Sprouts were identified by phenotypic characteristics of their leaves described by Gleason and Cronquist

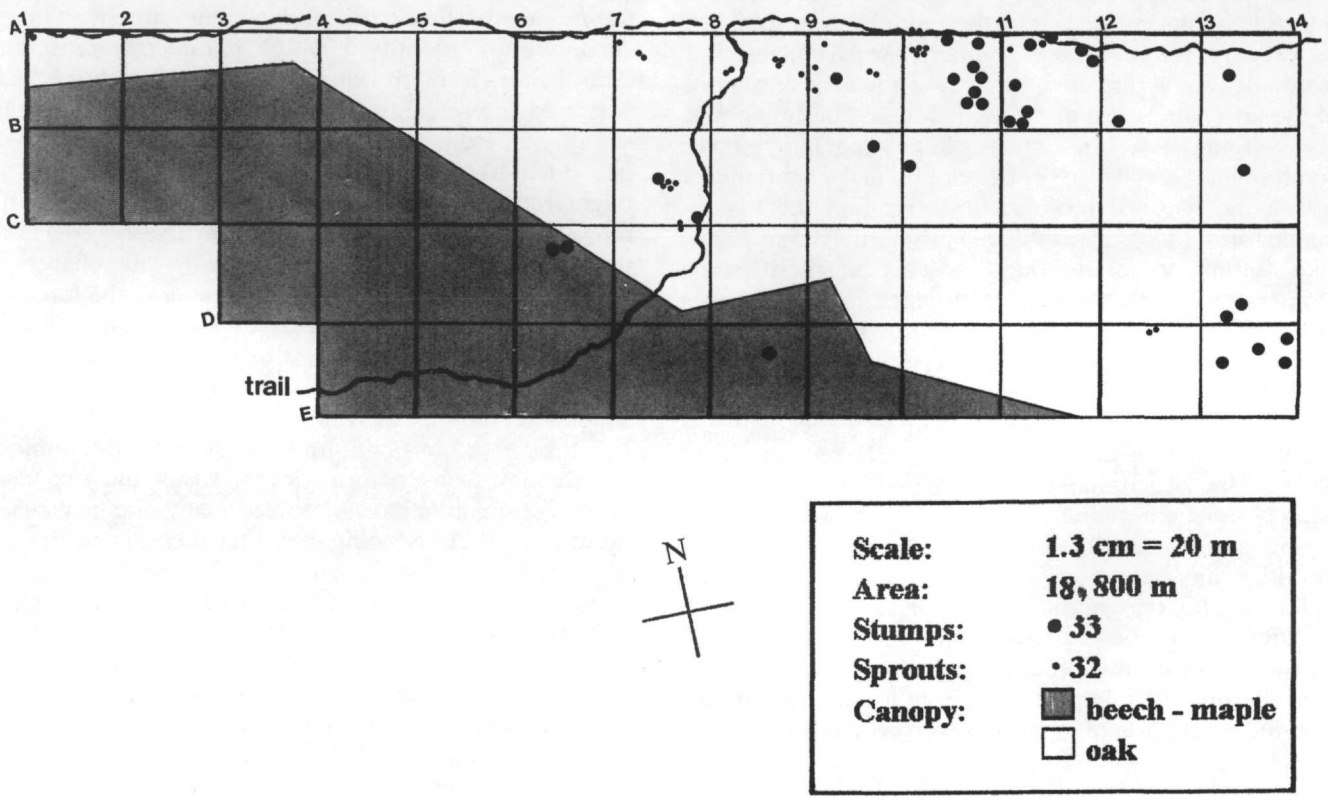

FIGURE 1. Distribution map of American chestnut stumps and sprouts over 18,800 m^2 at the Bedford site. The distribution of sprouts is aggregated under oak canopy and exhibits segregation from chestnut stumps.

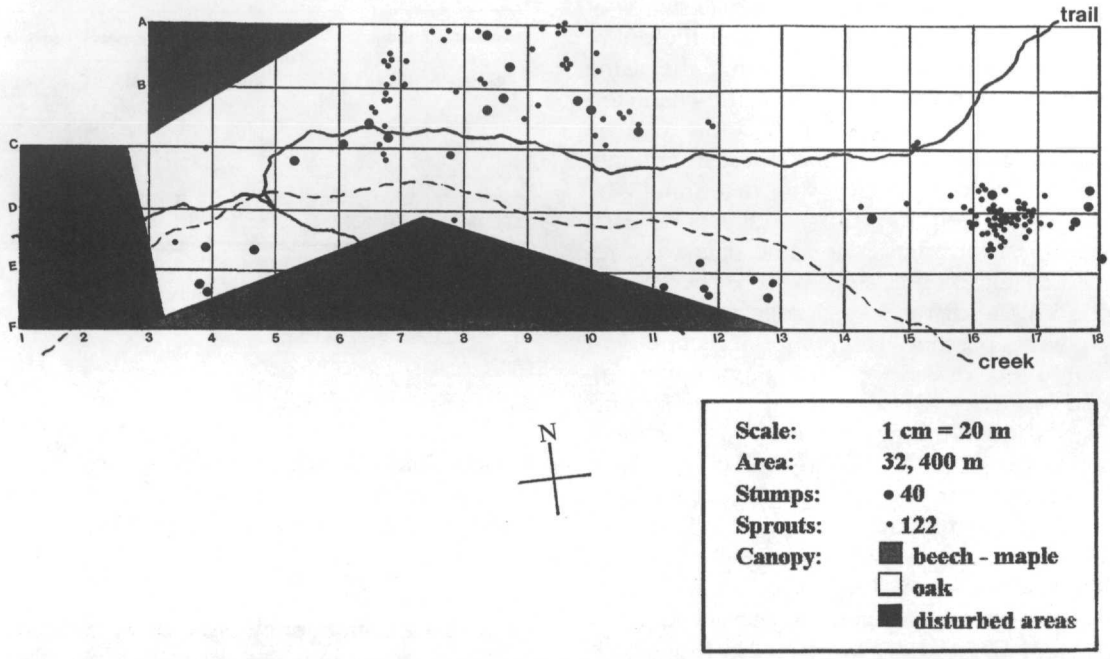

FIGURE 2. Distribution map of American chestnut stumps and sprouts over 32,400 m² at the Brecksville site. The distribution of sprouts is aggregated under oak canopy and exhibits segregation from chestnut stumps. (Areas marked as "disturbed" in the legend reflect land undergoing selective cutting and prescribed burning for the purpose of oak forest restoration by the Cleveland Metroparks.)

(1991) and by Bailey (1949) as serrate with ascending incurved teeth, glabrous, acuminate, and cuneate at the petiole. Each stem was counted as a single sprout, unless it was growing from the base of another stem above the soil. Chestnut stumps were initially identified by qualities such as wood grain and toughness, humus color, and characteristic hollowing (Panshin et al. 1964). Samples of wood with dimensions approximating 2 cm x 2 cm x 5 cm were cut from the stumps. Tangential sections were then taken from these wood samples to view cellular structure. Chestnut can be positively distinguished from oak (the only other likely ring-porous alternative in these woods with similar decay patterns) by examining the presence or absence of multiseriate rays of the secondary xylem. Oak has characteristically large, multiseriate rays in addition to much smaller, uniseriate rays. Chestnut xylem contains only uniseriate or biseriate rays (Esau 1961, Titmuss 1959, Walker 1989). The sections were boiled for several minutes to soften the tissue and placed on a slide with a drop of Hoyer's medium. The slides were observed at 10x and compared with wood samples made available by the National Lumber Manufacturer's Association. These samples of *Quercus alba*, *Quercus rubra*, and *Castanea dentata* served as the standard for determining the identity of each stump. Each stump and sprout identified was given a brass tag with a transect code and specimen identification number driven into the soil with acrylic coated spikes near the sprouts at a 4-6 cm distance. This tagging system was implemented for easy relocation by a metal detector for future study.

The following data were recorded for each stump: location with respect to the nearest grid point, basal diameter in centimeters, and the type of canopy and understory occupants found around the specimen. The

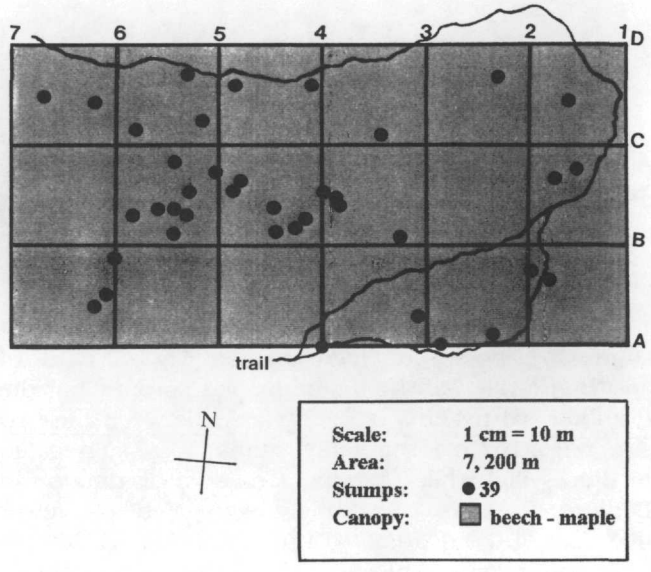

FIGURE 3. Distribution map of American chestnut stumps over 7,200 m² at the North Chagrin site. No sprouts were observed at this location.

dominant canopy species above each specimen was assessed by determining which species over the specimen received direct sunlight in an approximated area of 10 m diameter. A general canopy portrait of the entire grid was determined at each site by using the same method over each grid point. In this way, the characteristic canopy cover over each specimen could then be compared to the canopy cover of the forest in general. The dominant understory species was determined by noting which species were most abundant around each specimen within a 5 m radius. The same data were recorded for sprouts, except that sprouts were checked for blight infection if the distinctive orange perithecia of *C. parasitica* were present. Degree of infection was noted as either 'initial' or 'severe' according to the number of affected branches. Because many of the sprouts are relatively small with few branches, two or more blighted branches constituted 'severe' infection. There were also categories for healthy sprouts, those with healthy green leaves and no apparent perithecia extruding from the bark, and dead sprouts, which could usually, but not always, be contributed to the blight fungus. Each sprout was also assigned an age category: 1-3, 4-6, 7-10, 11-14, 15-20, and 21-30 years. Age was ascertained by counting bud scale scars on young stems (categories 1-3 and 4-6), which constituted 72% of all sprouts. Ages of older stems were estimated by size comparisons. The greater range in the older categories allows for accruing uncertainty.

From the data collected, distribution maps were drawn for each of the three grids to show the location of both stumps and sprouts. Distances at a scale of 1 cm = 10 m were calculated from every stump to its nearest neighboring stump. A similar measurement was taken from each sprout to its nearest neighboring sprout. From these data, the spatial distribution of stumps and sprouts was determined by the Clark-Evans nearest neighbor method following the formula Ra/Re, where *Ra* is the actual mean distance between neighbors and *Re* is the expected mean distance calculated by

$$\frac{1}{2\sqrt{d}}$$

and *d* is the number of sprouts divided by the total area of the grid (Clark and Evans 1954). Contingency tables and chi-square tests were then employed to test for spatial association between sprouts and stumps.

RESULTS

North Chagrin had the most dense population of stumps, yet no sprouts were located (Fig. 3). Bedford and Brecksville had both stumps and sprouts, but the distributional patterns of each varied between the two sites (Figs. 1, 2). Most notably, stumps were aggregated in Brecksville, while showing a random distribution in Bedford. Sprouts were strongly aggregated into fewer than half of the quadrats at both sites (Fig. 4). Results from contingency tables and chi-square tests revealed a tendency for stumps to be closer to other stumps, while sprouts were found near other sprouts (Fig. 5).

	NORTH CHAGRIN		BEDFORD		BRECKSVILLE	
	stump	*sprout*	*stump*	*sprout*	*stump*	*sprout*
distribution	random		random	aggregated	aggregated	aggregated
Ra / Re =	.946 < 1		.892 < 1	.461 < 1	.625 < 1	.409 < 1
K =	.65 < 2.04		1.18 < 2.04	5.83 > 2.04	4.53 > 2.02	12.49 > 1.96
n =	39		33	32	40	122
c =	0.05		0.05	0.05	0.05	0.05

FIGURE 4. Summary of the spatial distribution of American chestnut stumps and sprouts at each of the study sites as determined by the Clark-Evans nearest neighbor method. No sprouts found at the North Chagrin site.

Information collected to assess canopy changes in relation to sprout location indicated a strong association of chestnut sprouts with oak canopy (Fig. 6). All three sites

2 x 2 contingency table of sprouts and stumps located in 47 quadrats at Bedford

	stumps present	stumps absent
sprouts present	4	5
sprouts absent	9	29

2 x 2 contingency table of sprouts and stumps located in 81 quadrats at Brecksville

	stumps present	stumps absent
sprouts present	12	11
sprouts absent	17	41

X^2 values from 2 x 2 contingency tables

	X^2	*p*	*df*	*alpha*
Bedford	1.57	3.84	1	0.05
Brecksville	3.75	3.84	1	0.05

FIGURE 5. Contingency tables used to derive chi-square values. The calculated values of 1.57 and 3.75 do not exceed *p*. Therefore, the hypothesis that sprout distribution is not dependent upon stump distribution is accepted.

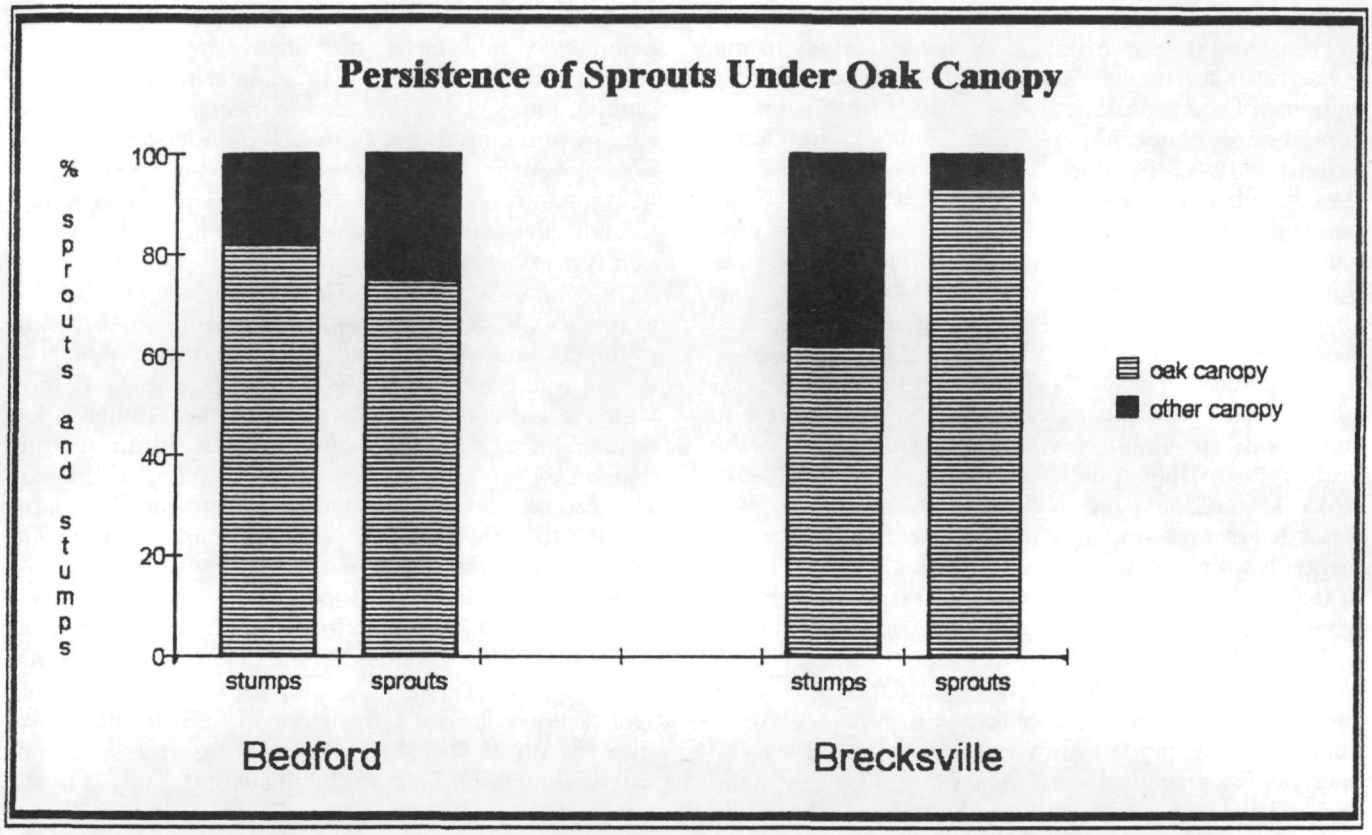

FIGURE 6. Graph depicts percentage of American chestnut stumps and sprouts found under oak canopy at the Bedford and Brecksville sites. North Chagrin's A. B. Williams Memorial Woods site had no sprouts. Bedford had 75% of the sprouts under oak canopy, which comprised approximately 76% of the total forest canopy. In Brecksville, 94% of the sprouts were found under oak, though only 59% of the site had oak as the dominant canopy species. See Figs. 1-2 for delineation of canopy transition at the Bedford and Brecksville sites.

showed a rather uniform understory of young beech and maple including those areas dominated with oak canopy that contain chestnut sprouts. After three years, a new search for sprouts at the same study sites yielded sprouting rates and death rates (Fig. 7).

DISCUSSION

Variations in chestnut stump and sprout distribution occur at all three sites. Several factors, such as the developmental stage of the forest within the study sites, past land use of these sites, and the size of the experimental grids, contribute to the apparent differences. Chestnut stumps, for example, were aggregated in Brecksville, but they were randomly distributed in Bedford and North Chagrin (Figs. 1-4). The random distribution of stumps in North Chagrin is a pattern associated with older, undisturbed forests, where competition eliminates many individual constituents until an equilibrium is achieved. If chestnut blight had never reached this area, the size of the chestnut stumps along with the current old-growth occupants indicates that this area would be a mixed hardwood forest with chestnut, beech, and sugar maple existing as codominants of the canopy, along with red oak limited to the most xeric spots and hemlock occupying valley slopes. Associations of chestnut and beech were found by Braun, usually in the mixed mesophytic forest region. Apparently the association can exist if chestnut already has a firm foothold in the forest, although the association is generally not the

	Bedford	Brecksville
# of original sprouts	32	122
# of sprouts dead after 3 years	6	20
# of new sprouts after 3 years	16	53
(%) death rate after 3 years	18.75%	16.39%
(%) sprout rate after 3 years	50%	43.44%
# of sprouts gained over 3 years	10 31.25%	33 27.05%

FIGURE 7. Summary of changes in number and health of American chestnut sprouts after three years at the Bedford and Brecksville sites. As indicated, there is an increase of sprouts at both sites by 31% and 27%, respectively. However, data regarding comparative vigor of the new sprouts to the old have not yet been collected.

norm of any major forest type (Braun 1950). The following description is by Arthur B. Williams, for whom this forest was subsequently named, noting the various constituents of the preceding forest (1949). "In this tension zone between beech-maple and hemlock, frequently extensive beech-hemlock associations were present. This was also the place where red oak, white oak, scarlet oak, and chestnut occurred." The understory is now almost exclusively beech and sugar maple. There is little doubt that the advance of the chestnut blight has changed the character of this forest and accelerated succession toward its climax of beech and maple.

The difference in stump distribution between Brecksville and Bedford must be explained by another reason since both areas show evidence of cultivation in the years prior to their purchase by the Cleveland Metroparks. The random pattern of chestnut stumps in Bedford is not that of a past old-growth forest, as these stumps are markedly younger than those in North Chagrin (Fig. 8). Instead, the site at Bedford contains secondary-growth where chestnut must have quickly re-established itself as a constituent as various lots were no longer cultivated. Purchase of these lands by Cleveland Metroparks afforded them protection from further disturbance. Aerial photos held by the park show portions of this area to be open field as recently as 1938. The present canopy at the Bedford site contains mostly red oak along with white oak and sugar maple. There is a transition in canopy type, however, from the northeast section toward the southwest section where a mixture of hardwoods exist, including young beech and maple trees, and where several pines have been planted next to the adjoining parking lot (Fig. 1). Though few beech trees reach the canopy in the northeast section, the understory contains a significant number of small beech stems among the heir-apparent population of sugar maple. Like North Chagrin, the forest at Bedford seems headed toward a beech-maple climax.

In contrast to the site at Bedford, clearing of the land at Brecksville's site was in part selective, because many of the chestnut stumps that remain are much older than the surrounding secondary-growth (Fig. 8) and most were not cut until the 1930s by the WPA. Though selection might explain an aggregated distribution rather than a random one, there is another factor to consider. The size of the experimental grid at Brecksville is large enough to show areas of topographic incongruity. The site actually covers portions of two ridgetops and the intervening lowland developed by a tributary of Chippewa Creek, which in turn feeds the Cuyahoga River. As discussed earlier and noted in the land surveys of northeast Ohio by Moses Cleaveland (1796) and more specifically described in the surveys of Brecksville Township by Alfred Wolcott, "oak growing in associations with chestnut and hickory dominate[d] the ridges of the Cuyahoga River Valley" (Wolcott 1811). Chestnut did not and does not occupy the lowland areas and thus the stumps are aggregated toward the two adjacent ridges.

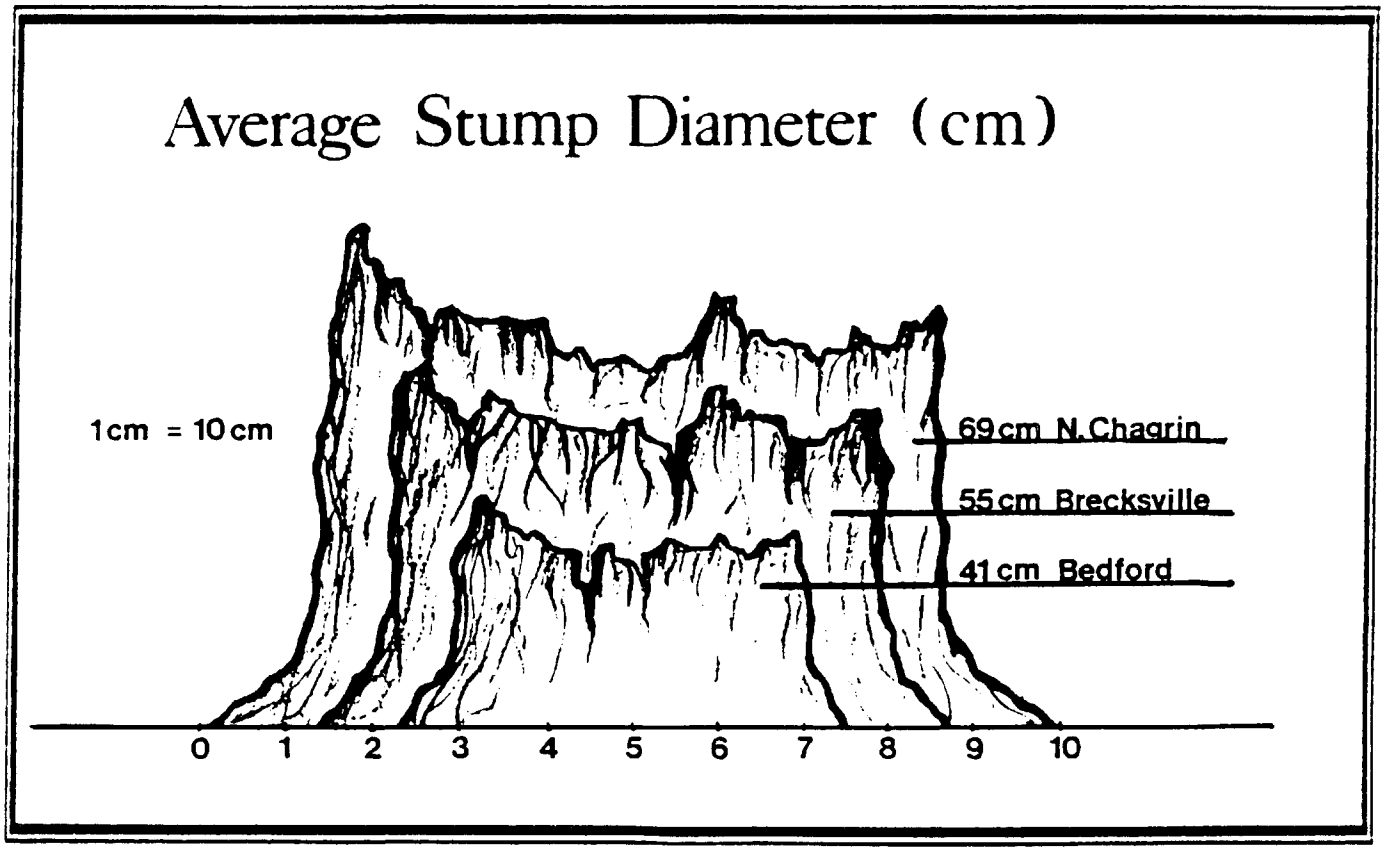

FIGURE 8. Tree ages can be generally inferred from the stump diameter measured and averaged at each of the study sites. The estimated ages of most of the stumps in North Chagrin and Brecksville date their existence well back into the 19th century. The stumps at the Bedford site are much smaller, establishing themselves in increasing pockets of land no longer farmed as the 20th century grew nearer.

Even though chestnut stumps are found on both ridgetops, the character of the canopy upon them is quite distinct. A transition occurs from woodland dominated by white oak in association with shagbark hickory along the ridge northeast of the creek to woodland containing significant numbers of beech that occupy the canopy on the ridge southwest of the creek (Fig. 2). Also noted is that the age of these beech trees appears somewhere between that of the old chestnut stumps and the secondary growth found throughout the northeast ridge based on average diameter growth rates of upland hardwood species reported by Ginrich (1967). The forest on the southwest ridge is also second growth, but its disturbance appears to be less recent than that on the northeast ridge, which follows Braun's contention that forest succession is generally set back by land use (1950). This setback in transition is only temporary, while the changes in soil due to agriculture, grazing, and fire suppression favor the more mesic species of beech and maple. Here, too, understory observations give clear indication that the future forest of these ridgetops will be a beech-maple climax association.

Distribution of chestnut sprouts, in contrast to the stumps, were strongly aggregated into fewer than half of the quadrats at Bedford and Brecksville, and were completely absent from North Chagrin (Figs. 1-4). The absence of chestnut sprouts at the North Chagrin site is consistent with observations made by Paillet in a study of chestnut distribution in southern New England woodlands (1988). Paillet attributed the absence of sprouts in the interior of old-growth forests that once contained numerous chestnut trees to competitive exclusion by more shade tolerant species on mesic sites. Bedford's sprouts are localized in a single area where the canopy is predominated by red oak (Figs. 1, 6). Sprouts in Brecksville are approximately divided with about half at one location and half densely aggregated at a second location (Figs. 2, 6). Both Brecksville locations are characterized by a uniform white oak canopy and, to a lesser extent, hickory. Similar to North Chagrin's absence of sprouts, transition areas in Bedford and Brecksville, where increased numbers of beech and maple occupy the canopy, also show lack of sprouts. A few sprouts occur near the tension zones, but even these neighbor oak.

Competitive exclusion explains the absence of sprouts under shade-tolerant species such as beech and maple, but it does not explain the aggregation of the sprouts in specific areas within a uniform oak canopy where sprouts seem to survive, nor does it explain the separation of sprouts from the remaining stumps (Fig. 5). The apparent uniformity of the oak-hickory association suggests that any variations in soil conditions throughout the area would not fully account for the strongly aggregated pattern of sprouts. Why sprouts are not distributed throughout the oak forests where chestnut was once a major constituent can be explained by differences in vigor of extant root crowns beneath the soil. Important to note is that sprouts were never located at the base of any stump, instead they were isolated or, more commonly, observed near the base of another sprout usually less than 10 cm in diameter. This distributional pattern supports the contention of Paillet that variations in chestnut sprout distribution reflect the distribution of chestnut seedlings at the time when chestnut blight destroyed mature chestnut trees, thereby diminishing the source of seed (Paillet 1984, Keever 1953). Basic to this argument is that older chestnut trees, especially those over 100 years, have less sprouting ability than young trees, and that sprouting generally continues longer from root crowns originated from seed than from those of previous sprouts (Matoon 1909).

Thus, the energy available for sprouting within a root system declines with age and with each subsequent generation of sprouts, unless energy is replaced by the most recent sprouts. Results from contingency tables show that the current location of chestnut sprouts in Bedford and Brecksville is not entirely contingent upon remnant stumps and roots of larger chestnut trees. Instead, distribution is consistent with that observed by Paillet, and may reflect the distribution of chestnut seeds dispersed from the parent trees during the years just prior to the blight epidemic, which reached northeast Ohio in the early 1920s. Nothing remains of these seedlings but a persistent cycle of blight infection and subsequent sprouting.

After three years, changes were observed in the number of sprouts at the Bedford and Brecksville study sites (Fig. 7). The approximate 30% increase of sprouts at each of the two sites takes into account the death of some of those originally observed. All of the new sprouts were located near original ones, which supports the conclusion that sprouts are originating from remnant root systems of seedlings or saplings rather than remnants of mature trees. The observation that there has been an effective gain in the number of sprouts after three years is consistent with previous records showing a steady increase since 1930 in the basal area of active chestnut root crowns of Connecticut forests (Stephens and Waggoner 1980). Such increases hint that a degree of stability has been achieved in the American chestnut population. However, without comparative data regarding vigor of the new sprouts versus the old, conjecture about the significance of such an increase is arguable, and the future of the species appears as unclear as ever—particularly in the transitional forests of northeast Ohio.

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LITERATURE CITED

Anagnostakis, S. L. 1990 Improved chestnut tree condition maintained in two Connecticut plots after treatments with hypovirulent strains of the chestnut blight fungus. Forest Science 36: 113-123.

—— 1987 Chestnut blight: The classical problem of an introduced pathogen. Mycologia 79: 23-37.

Bailey, L. H. 1949 Manual of Cultivated Plants. MacMillan Publishing Company, Inc., New York, NY. 232 pp.

Braun, E. L. 1950 Deciduous Forests of Eastern North America. The Blakiston Company, Philadelphia, PA. pp. 11-528.

Clark, P. J. and F. C. Evans 1954 Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35: 45-53.

Cleaveland, M. 1796 Report to Connecticut Land Co. Western Reserve Historical Society, Cleveland, OH. MS 3233.
Esau, K. 1961 Anatomy of Seed Plants. John Wiley and Sons, Inc., New York, NY. pp. 95-112.
Ginrich, S. F. 1967 Measuring and evaluating stocking and stand density in upland hardwood forests in the central United States. Forest Science 13: 38-52.
Gleason, H. A. and A. Cronquist 1991 Manual of Vascular Plants of Northeastern United States and Adjacent Canada. D. Van Nostrand Company, Inc., Princeton, NJ. pp. 247-248.
Hebard, F. V. 1982 Biology of virulent and hypovirulent *Endothia parasitica* on American chestnut (*Castanea dentata*). Ph.D. dissertation, Virginia Polytechnic Institute and State University, Blacksburg, VA. pp. 295.
Keever, C. 1953 Present composition of some stands of former oak-chestnut forest in the southern Blue Ridge Mountains. Ecology 34: 44-55.
Matoon, F. E. 1909 The origin and early development of chestnut sprouts. Forest Quarterly 7: 34-47.
Merkel, H. W. 1905 A deadly fungus on the American chestnut. New York Zoological Society, 10th annual report. pp. 97-103.
Nash, S. 1988 The blighted chestnut: New research races with time to recover a great American tree. National Parks 62: 12-18.
Paillet, F. L. 1988 Character and distribution of American chestnut sprouts in southern New England woodlands. Bull. Torrey Bot. Club 115: 32-44.
___ 1984 Growth form and ecology of American chestnut sprout clones in northeastern Massachusetts. Bull. Torrey Bot. Club 111: 316-328.
Panshin, A. J., C. De Zeeuw, and H. P. Brown 1964 Textbook of Wood Technology, Vol. 1. Structure, Identification, Uses and Properties of Commercial Woods of the United States. McGraw-Hill, New York, NY. pp. 559-570.
Peattie, D. 1950 A Natural History of Trees of Eastern and Central North America. Houghton Mifflin Company, Boston, MA. p. 189.
Sears, P. B. 1930 A record of post-glacial climate in northern Ohio. Ohio J. Sci. 27: 213-231.
Shapiro, R., G. H. Choi, and D. L. Nuss 1991 Virus-like genetic and expression strategy for double-stranded RNA genetic element associated with biological control of chestnut blight. The EMBO Journal 10: 731-739.
Stephens, G. R. and P. E. Waggoner 1980 A half century of natural transition in a mixed hardwood forest. Conn. Agr. Exp. Sta. Bulletin 783: 43.
Titmuss, F. H. 1959 A Concise Encyclopedia of World Timbers. The Technical Press LTD., London. pp. 75-159.
Walker, A. 1989 The Encyclopedia of Wood. Quarto Publishing, London. pp. 23-29.
Williams, A. B. 1949 The Native Forests of Cuyahoga County, Ohio. Cleveland Museum of Natural History, Cleveland, OH. pp. 12-32.
Wolcott, A. 1811 Field Notes of Brecksville Township Land Survey. Western Reserve Historical Society, Cleveland, OH. MS 75.